PHENOLOGY OF SPECIES COMMON TO THREE SEMI–ARID GRASSLANDS

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Synopsis

Australian phenological studies are reviewed briefly before presenting data on the leafing phenology of seven species and the flowering phenology of 25 species common to (i) a *Danthonia caespitosa* grassland on Riverina clay, (ii) a *Stipa variabilis-D. caespitosa* grassland on Billabong clay, and (iii) a *Stipa aristiglumis-D. caespitosa* grassland on Deniboota loam. Data were collected for 1952 (annual rainfall 18·4 in.) and 1953 (annual rainfall 12·9 in.). The disclimax grasslands adjoin on a level depositional plain situated in the south-west of New South Wales.

The differences in leafing phenology of a species common to the three grasslands appear to be related to soil differences such as permanent wilting percentage (15-bar value) and water-holding capacity. This is more evident for warm-season species than for cool-season species.

The growth-rhythms of the short-lived annual plants, which include many exotics, and the autumn- to spring-growing perennials indicate that the three disclimax grasslands are in equilibrium with the present annual climatic cycle. The remaining few perennial plants which respond to summer rainfall are related to, or are the indigenes of, the original communities from which the grasslands have developed.

In those species which bloom once in the spring-early summer period, the onset of flowering appears to be related in part to day-length change. For most species the difference in the date of the onset of flowering between years in the one grassland appears to be greater than the differences between grasslands. Those species which have more than one flowering period do not exhibit a fixed relationship between day-length in spring-early summer, and day-length at the commencement of any other bloom period.

It is concluded that the difference between the grasslands is found more in differences in the number of individual plants of each species and in the leafing phenology of the warm-season species common to the three grasslands, than in differences in species composition and in the flowering phenology of those species with only one bloom period.

INTRODUCTION

Moore (1880), in his Anniversary Address to the Royal Society of New South Wales, asked pastoralists to collect information on the habitat, vegetative and flowering performance of plant species on their sheep and cattle runs. No useful data appear to have been collected. Haviland (1886) compiled eight lists of indigenous species found about Sydney, N.S.W., and recorded the months in which they were in bloom. Maiden (1909) published a short bibliography of Australian phenological literature.

Heyward (1931) constructed a phenological record for all 554 indigenous Victorian genera using herbarium records supplemented by personal observations. She noted that most species did not vary their flowering dates by more than a few weeks even though temperature, rainfall, or elevation varied substantially. After discussing the importance of environmental factors in natural selection, and in particular the influence of the dry, hot summer, Heyward concluded that no single factor could be the sole determinant of time and duration of flowering. In this study the flowering periods of all species in a genus were combined to give a generalized picture.

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Patton (1933) recorded the number of species flowering in each month on a heath at Cheltenham, Vic. He noted the large spring peak of bloom, that several indigenes performed exceptionally by flowering in summer, and that summer rainfall seldom elicited a plant response because of high evaporation. Patton (1936) recorded a similar late spring peak of bloom in an indigenous tussock grassland near Melbourne, Vic.

Biddiscombe *et al.* (1954) reported leafing and flowering phenology of the major perennial grasses and winter-growing herbs in a disclimax grassland at Trangie, N.S.W. The first detailed list of flowering dates for individual species in an Australian community was reported by Specht and Rayson (1957) for the heath near Keith, S.A. Derrick (1962) presented charts for all Australian States (excluding the Northern Territory) which show the approximate flowering season of many common indigenes and exotics. Groves and Specht (1965) have presented flowering times for two areas of heath vegetation at Wilson's Promontory, Vic., and Groves (1965*b*) for indigenous and naturalized species in a *Themeda* tussock grassland at St. Albans, Vic.

The first report on both flowering and leafing phenology for more than one year was presented by Williams (1961) for a number of species in a *Danthonia caespitosa* grassland on Riverina clay at Deniliquin, N.S.W. In the present paper the 1952 and 1953 data on leafing and flowering phenology of selected species in this grassland are compared with the same species in two adjoining semi-arid grasslands, *Stipa variabilis-D. caespitosa* on Billabong clay, and *S. aristiglumis-D. caespitosa* on Deniboota loam. The data are considered in relation to estimates of the periods during which soil water is available for plant growth. Differences and similarities in phenology are discussed. Climate is common to all three communities because they adjoin, trees are absent, short-grasses and herbs predominate, and the general topography is featureless.

ENVIRONMENT

Climate

Detailed characteristics of the Deniliquin climate have been presented previously (Williams, 1956). The seasons are taken as summer (December to February), autumn (March to May), winter (June to August), and spring (September to November). The mean annual rainfall is 15·8 in., and cool-season rains are more reliable than summer rains.

Rainfall recorded in 1952 and 1953 at the meteorological station proximate to the three sites is set out in the lower part of Fig. 1 as in./15 days. In 1952 the annual rainfall was 18·4 in., or 10% above average, while in 1953 it was 12·9 in., 23% below average.

Summers are hot, with occasional thunderstorms. January is the hottest month, with a mean maximum temperature of 89·5° F. and a mean minimum of 61° F. From January to March, 1952, there were 34 days, and from October to December eight days with maximum temperatures in excess of 90° F. The corresponding values in 1953 were 33 and 14 days.

Winters are cool. In both 1952 and 1953 there were approximately 30 light frosts (screen temperature >32° <36° F.) and 16 severe frosts (screen temperature <32° F.).

Day length (civil twilight) at the experimental site ranges from a maximum of 15 hours in December to a minimum of 10 hours in June.

In summary, incidence and quantity of rainfall and the period of heavy frost were the factors which differed most markedly between the two years.

Soils

(i) Topography and general distribution

The topography and soils of the general area have been described by Churchward (1958). The three experimental sites are located at the C.S.I.R.O.

Falkiner Memorial Field Station, the *D. caespitosa* and *Stipa variabilis-D. caespitosa* grasslands on the lower and upper levels of the clay plains, and the *S. aristiglumis-D. caespitosa* grassland on the loam of the Stud Park River Ridge.

(ii) Soil-types

The soils at each site are similar to those described and named by Smith (1945), Butler and Johnston (1946), and Johnston (1953) as Riverina clay, Billabong clay, and Deniboota loam.

Riverina clay is a grey clay (Stace *et al.*, 1968, p. 79) with a 0–0·5 in. A horizon of slightly structured light clay which is hard when dry and sticky when wet. The B_1 horizon of 0·5–10 in. is a moderately structured heavy clay overlying grey poorly-structured heavy clay. The permanent to semi-permanent cleavage planes extend to the surface. All three components of the gilgai micro-relief, the puff, shelf and depression are represented (Williams, 1955).

Billabong clay is a brown clay (Stace *et al.*, 1968, pp. 79, 103) with a 0–0·5 in. A horizon of grey-brown compacted clay loam which is hard when dry and sticky when wet. The B_1 horizon of 0·5–12 in. is a dark grey-brown massive heavy clay with blocky structure. It is hard when dry and intractable when wet. Below 12 in. the soil is a poorly-structured heavy clay. Cleavage planes are few and rarely extend to the surface. There are few areas of puff, and a small amount of depression.

Deniboota loam is a red-brown earth (Stace *et al.*, 1968, pp. 211, 214) with a 0–3 in. A_1 horizon of brown loam which is hard when dry and friable when wet. The A_2 horizon is 3–6 in. of grey-brown sandy clay loam which is slightly compact and hard when dry but friable when wet. The B_1 and B_2 horizons from 6–24 in. are medium clays with well developed medium prismatic structure grading into grey-brown clay.

The main chemical differences between the three soils in the top 24 in. are (1) the acid reaction of the Billabong clay and Deniboota loam surfaces compared with the alkaline reaction of the Riverina clay (pH 6·1, 6·5 *v.* 7·5) and the pronounced alkaline reaction (pH 8·8) of the loam below 9 in., (2) the small amount of chloride in the Deniboota loam profile compared with the amounts in the Riverina and Billabong clays (0·034 *v.* 0·237 and 0·206 at the 9–18 in. depth, expressed as NaCl per cent. oven dry weight).

The differences in nitrogen and phosphorus status between the various surface soils are small, with a range of 0·052 to 0·100% and 0·017 to 0·020% respectively.

Both calcium and magnesium on the exchange complex of Riverina clay greatly exceed the values obtained from Deniboota loam (13·98 *v.* 2·27 and 14·05 *v.* 1·92 m-equiv./100 g. oven dry weight).

(iii) Soil moisture relationships

The periods over which water in the 0–3 and 3–9 in. depth is available for plant growth are set out in the lower part of Fig. 1, together with a record of the sampling dates and the incidence of rain sufficient to raise the moisture content of the 0–3 in. depth to the 15-bar level and above for short periods between sampling dates. These periods were calculated for the various depths by gravimetric determinations of soil moisture for two sites in each gilgai component on the clay soils, and at two sites in the loam, 15-bar values for each depth, and bulk densities for the soil horizons. Slivers of wet soil were taken from the sides of cracks after rain and the soil water content determined.

The amount of water which raised the moisture content of the surface 0–3 in. from the minimum field value to the 15-bar value ranged from 0.08 in. for Deniboota loam, $0 \cdot 28$ and $0 \cdot 40$ in. for the shelf of Riverina clay and Billabong clay, to $0 \cdot 50$ and $0 \cdot 56$ in. for the depression of the Riverina clay and Billabong clay. Small amounts of rain are sufficient to provide available water in the surface of Deniboota loam.

The available water within the maximum wetted profile over the 1952–53 period ranged from $4 \cdot 3$ in. in the Deniboota loam, $1 \cdot 7$ and $1 \cdot 0$ in. in the depression and shelf of the Riverina clay, to $0 \cdot 8$ and $0 \cdot 4$ in. in the depression and shelf of Billabong clay.

In 1952 the Deniboota loam had available water in the 0–3 in. depth for 270 days, the Riverina clay for 260 days (depression) and 240 days (shelf), the Billabong clay for 220 days (depression) and 140 days (shelf). In 1953 these periods were shortened by from 70 to 110 days.

Depressions tend to be wetter than 15-bar values, *per se*, indicate because depressions are recipients of run-off from the massive surface of the neighbouring shelf. Further, run-off into cleavage planes modifies the generalized available water situation because it produces localized pockets of wet soil at depth. Water penetration is more uniform in Deniboota loam.

Vegetation

The three grasslands appear to differ markedly from the original communities of 100 years ago.

(i) *Danthonia caespitosa* grassland.

This grassland has been the subject of several papers (Williams, 1955, 1956, 1961). It has developed from an *Atriplex nummularia* Lindl. shrub-steppe community, possibly by way of an *A. vesicaria* Hew. ex Benth. community.

The last *A. vesicaria* plants were eliminated from the experimental area by sheep grazing in 1948.

(ii) *Stipa variabilis-Danthonia caespitosa* grassland.

This grassland appears to have developed from the *Acacia pendula-Atriplex nummularia* association (Moore, 1953a, pp. 514–5). Few areas of unmodified shrub woodland now exist.

The present grassland has been described by Moore (1953b, p. 561) as a disclimax community, and Williams (1956) has measured its botanical composition. Of the original dominants, only scattered plants of *Kochia aphylla* R.Br. remain.

(iii) *Stipa aristiglumis-Danthonia caespitosa* grassland

This grassland is a disclimax community at the western margin of the *Eucalyptus woollsiana-Callitris columellaris* association within the *E. woollsiana* alliance (Moore, 1953a, p. 508). Small areas of the original savanna woodland still exist to the east of the Field Station.

The present grassland developed under intensive sheep grazing and the felling of trees for drought-fodder, structural timber or firewood.

PROCEDURE

The procedure followed the pattern of the previous study (Williams, 1961), with the frequent recording of species behaviour within a fixed area in each of the three grasslands. These observations were made monthly, or more frequently, e.g. every two or three days, when plants were flowering.

The commencement of leafing, onset and duration of flowering and leaf senescence were recorded for each species. The periods when plants were

vigorously vegetative, or were making limited leaf growth were estimated using plant height, plant diameter, or leaf length, appropriate to the growth habit of the particular species. Recording commenced in mid-1951 and continued until the end of 1954. Confirmatory checks of bloom periods were made between 1956 and 1961.

Soil sampling was started in mid-1951 and continued until the end of 1953. The two years 1952 and 1953 with coincidental vegetation and soil moisture data are used in this paper.

RESULTS

The phenological data are presented in two sections : (a) the leafing phenology of seven species common to all three grasslands in 1952 and 1953, and (b) the flowering phenology for 25 common species during the same period.

(a) Leafing Phenology

Figure 1 illustrates the leafing phenology of seven species chosen because there were complete records for both soils and years and because they illustrate the behaviour of many species in the grasslands. Rainfall, frost periods and periods of available water in the 0–3 and 3–9 in. depths for each site are shown for 1952 and 1953.
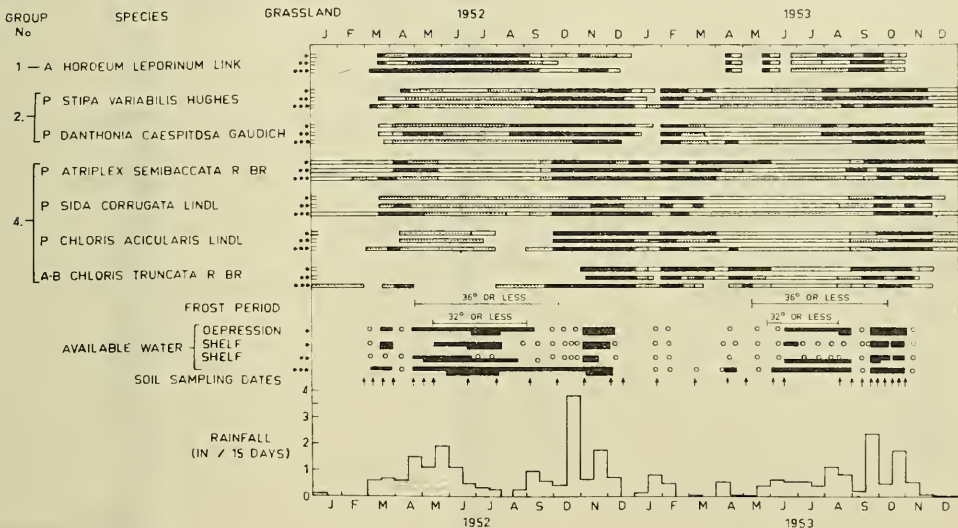

Fig. 1.

The three groups are numbered 1, 2, and 4, and are arranged as previously described (Williams, 1961) in the order of predominantly cool-season growth, through growth in all seasons, to predominantly warm-season growth. Groups 3 and 5 are omitted because they contained no species which grew continuously on all three soils in each year.

The difference between the sites is illustrated by the performance of species as follows : Deniboota loam and the depressions in Riverina clay tend to maintain green leaf longer, as with *Hordeum leporinum* in spring and early summer, than do the other soils. In Group 2–1952 *Stipa variabilis* tends to start growth first in Deniboota loam, then Billabong clay, and Riverina clay. In Group 4 there were differences in species behaviour on the three soils, e.g. *Atriplex semibaccata* (May, 1953), *Sida corrugata* (January-February, 1952), *Chloris acicularis* (March,
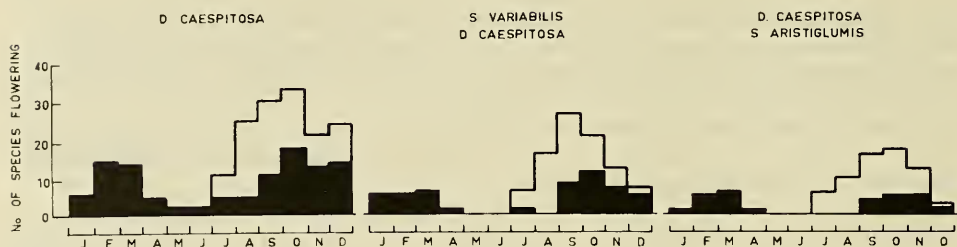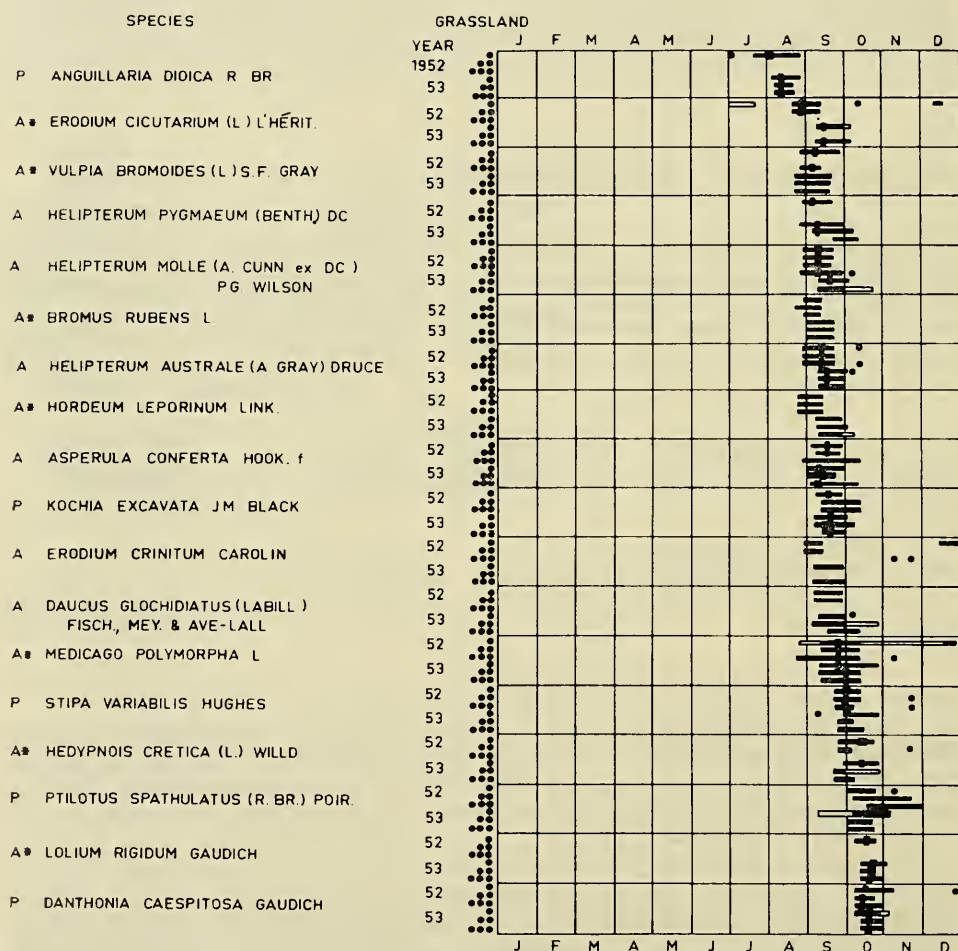
Fig. 2.

Fig. 3.

1952), but more particularly *C. truncata* (January to April, 1952 ; August to October, 1952 ; and September to November, 1953).

The growth differences between 1952 and 1953 were substantial. In 1952 active growth commenced in mid-March, but in 1953 there were two false starts, and the species in Group 1 did not commence active growth until the end of June. The heavy rainfall in October, 1952, with the vigorous leaf-growth of Group 4 species, which continued until the end of December, contrasts strongly with the tapering off in the growth of these species at the conclusion of the 1953 spring. Low winter temperatures and frosts do not prohibit leaf growth in Groups 1 and 2.

Years in which the soil moisture is low in autumn and winter, as in 1953, are not unusual.

(b) *Flowering Phenology*

(i) Flowering rhythms

In Fig. 2 the flowering rhythms of the three grasslands are set out. The maximum number of species observed flowering in each particular month of the two-years experimental period has been used to construct this figure.

A feature of these flowering rhythms is the contribution made by species that have more than one bloom period.
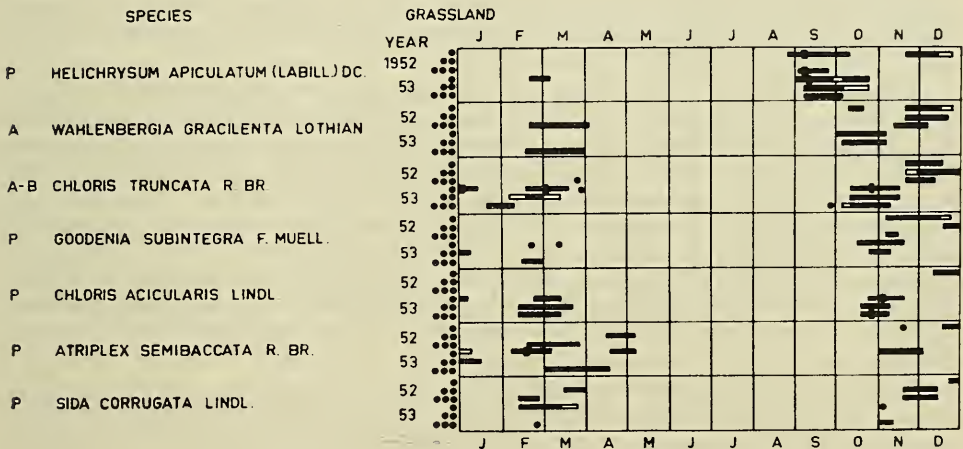

Fig. 4.

(ii) Flowering dates

The flowering dates for species common to the three grasslands are set out in Figs 3 and 4.

Figure 3 summarizes the records for 18 species which have consistently exhibited one main bloom period between July and December, but at no other time. They are arranged in order of flowering. Most plants in these disclimax grasslands belong to this category.

The onset of the main bloom period differed between soils for *Ptilotus spathulatus* in 1952, *Helipterum pygmaeum* in 1953, and to a lesser degree for *Helipterum molle* and *Daucus glochidiatus* in 1953. It differed between years for *Helipterum australe* and *Hordeum leporinum*. Though the bloom periods of some species, e.g. *Hordeum leporinum* started earlier in 1952 than in 1953, other

species, e.g. *Vulpia bromoides*, behaved in the opposite manner.   Peak bloom in 1952 was generally a few days to a week earlier than in 1953.

Species which may exhibit one bloom period between July and December, and another in summer and autumn, cause the February to April peak in Figure 2. The flowering periods of seven species in this group, arranged in order of spring flower appearance, are shown in Fig. 4.

The onset of the spring bloom period differed between years for *Wahlenbergia gracilenta* and *Chloris truncata*.   Differences between the soils in either 1952 or 1953 were seldom greater than one week for these species, but up to six weeks for species such as *Goodenia subintegra*.

Summer and autumn flowering varies markedly between years, and, with the exception of *Chloris acicularis*, between soils in the one year.

DISCUSSION

Leafing Phenology

Differences in leafing phenology of common species in the three grasslands are apparent in early 1952 in the *S. aristiglumis-D. caespitosa* grassland, where there was a tendency for Group 1 species to start growth first and for the Group 4 species to maintain vigorous growth over a longer period than in the other two grasslands.   This performance was repeated in late 1952, but not in late 1953.

The summer-growing species of Group 4 are rather irregular in their performance, because they depend on the erratic summer rains.   Even so, there are several important differences between the grasslands for species such as *Sida corrugata* and *Chloris truncata*.

These differences are attributed to differences in soil water between Deniboota loam, Billabong clay and Riverina clay, and in particular, to the low 15-bar value, high permeability, and large water-holding capacity of Deniboota loam relative to the other soils.   The crude nature of the relationship between the overall leafing phenology and available water in Fig. 1 reflects the inadequacy of the gravimetric method for determining moisture in soils which rains penetrate unevenly and roots do not exploit uniformly.   The relationship between the drying cycles and the leafing phenology is particularly unsatisfactory.   It is noteworthy that the more successful studies of this type have been recorded on permeable soils in regions of pronounced seasonal rainfall (Specht, 1957).

The pattern of vegetative growth in 1952 and 1953 illustrates the performance in a long and a short season ; performances which occur frequently over large tracts of southern Australia.   There is nothing atypical in the two false starts of the 1953 season and the associated contrast in leafing phenology between annuals and perennials.   Heavy rain makes moisture available for germination or growth on all three soils, whereas a light rain elicits a response only from the loam soil.

Specht and Rayson (1957), in their studies of the vegetative performance of heath species at Dark Island, South Australia, reported that, as expected in southern Australia, the geophytes made maximum growth in spring. However, some perennial components of the heath grew during hot, dry summers on soil water stored from the preceding winter-spring rains.   Occasional ineffective rain, or rare effective storms between December and March, do not appear to upset the notion that this lack of a relationship between the vegetative growth cycle of the dominant perennial (*Banksia ornata*), and the present rainfall regime is due to a long-term shift in climate (Specht and Rayson, 1957 ; Specht, 1958). These summer-growing species maintain vegetative growth patterns which are possibly characteristic of this previous climate.   Burbidge (1960) has commented

upon this out-of-phase characteristic for *Eucalyptus* and *Banksia* spp. in Western Australia, and Johnston and Briggs (1963) for Proteaceae. It is likely that these rare effective storms, together with impoverished soils, frequent burning, and the low intensity of grazing by introduced herbivores have been important in maintaining the dominants at Dark Island.

Groves (1965a) has recorded the maximum growth-rate of Victorian heaths in summer, from December to March, and of *Themeda* tussock grassland (Groves, 1965b) from October to early December. He contrasted these performances with the performance of a sown pasture of *Lolium perenne* and *Trifolium subterraneum*, which exhibited a maximum growth-rate from August to September (Twentyman, 1938). Groves commented further that the productivity of the *Danthonia* spp. in the *Themeda* grassland suggests that a *Danthonia* grassland may reach its maximum growth-rate some months before the *Themeda* community. Within most communities studied so far there are species groups which do not conform to the general community pattern. For example, Holland (1968), in seasonal growth studies in mallee communities in central New South Wales and western Victoria, has shown that tall shrubs and mallee eucalypts *do* make summer growth, but field layer plants do not. The three grasslands in the present study contain a wide range of phenological performances which similarly preclude a statement as to the particular community growth-rhythm.

In the Riverine plain the original communities appear to have been dominated by species with potential growth-rhythms of the warm-season type. From 1845 onwards these communities have been shaped by the process of species elimination, species invasion under the influence of sheep, rabbits, various other herbivores, and intermittent droughts (Williams, 1968). These processes have favoured the plants that can complete their life-cycle within the more reliable rainfall period from May to October, resulting in either the dominance of indigenes which can cope with the new conditions or the dominance of annual and perennial species of the Mediterranean type, or a mixture of the two groups. The remaining species are wholly, or partly, opportunist and rely on the erratic summer rains. Amongst the wholly opportunist species is *Chloris truncata*. Perennial species such as *Chloris acicularis* represent the vegetative pattern of the type of indigene which dominated the original communities. In spite of the wide-ranging root systems of these perennial indigenes, the growth pattern is not as regular as that of the heath dominants described by Specht and Rayson (*loc. cit.*), doubtless because soil moisture storage and rooting depth, even in Deniboota loam, are limiting on more occasions than they appear to be under heath vegetation. Thus each of the three communities expresses a wide range of species phenology. The exact form of this vegetative phenology is influenced by micro-topography, soil water differences between the grasslands, and different rainfall between years.

Flowering Rhythms

The flowering rhythms of the two species groups in each of the three grasslands are similar (Fig. 2). They appear to have counterparts in *Themeda* grassland (Groves, 1965b) and in southern heaths (Specht and Rayson, 1957 ; Groves and Specht, 1965), but not in montane communities in New Zealand (Scott, 1960 ; Clarke, 1968).

In the Riverine plain this two-population situation probably reflects the partial species elimination and concurrent invasion of species discussed previously.

Flowering Phenology

It has already been suggested (Williams, 1961) that the regular onset of bloom for spring flowering species of the *Danthonia caespitosa* grassland may be attributed in part to changes in day-length. This suggestion appears to be valid for these species in the other two grasslands.

Plasticity in vegetative characteristics does not appear to extend to flowering phenology. At best, a large vegetative response may promote a small flowering response in bloom period, but no shift in date of first bloom has been noted so far. Extended, or additional bloom periods in such annual species as *Medicago polymorpha* and the two *Erodium* spp. appear to be due to progressive flowering in favoured sites and the presence of more than one age group in the population.

The processes of species elimination and invasion, coupled with the reliable rainfall period in winter and spring, have favoured annual or perennial species of the Mediterranean type. By seeding profusely before the end of October, with or without hard-seed production, these species maintain themselves in the community.

The species which can flower in spring-summer and at other times are ephemerals of the *Wahlenbergia gracilenta* type or long-lived perennials of the *Chloris acicularis* type. An examination of the dates of first bloom has shown that the spring and autumn photoperiodic range for individual species is wide under natural conditions, and critical investigations using clones, transplants and field irrigation are needed.

The frequent-flowering perennials at Deniliquin are important from the ecological viewpoint because they are either remnants of the indigenes which dominated the original communities or are similar to them in leafing and flowering phenology. Their population density is low, as might be anticipated in a pastoral zone. This also appears to be the case at Trangie (Biddiscombe, 1953).

In principle, the maintenance of a plant in a community depends upon the longevity of the plants, the opportunity during that life-span to produce viable seed, the viability of the seed in the soil, and the opportunity to germinate and establish. Flowering, *per se*, may not mean much for trees and long-lived shrubs, but will mean a great deal for annuals (Holland, 1968). It will be critical in the early stage of colonization by a new species, becoming less important as the seed supply in the soil builds up and the area colonized increases.

Until the advent of domestic stock, there seems to have been scant advantage for the indigenes to produce seed or to possess superlative seedling vigour, because the parent plants were long-lived. In contrast, today there is a survival advantage in heavy spring seeding, in leaf-growth during the reliable rainfall period, and possibly in a limited vegetative response to out-of-season rainfall. Although the grazing pressures applied to the communities should favour earlier flowering through changes in botanical composition, the erratic summer storms support a counter movement. Herein lies one more reason for the difficulty in manipulating grasslands of this type by grazing, *per se* (Williams, 1969).

It is concluded that differences between species common to the three grass-lands are found to some degree in leafing phenology, particularly the leafing of the warm-season species, and to a more limited degree in the flowering phenology. The substantial difference between grasslands is not found so much in representation by different species or in the flowering phenology of those species common to the grasslands, as in the number of individuals of each species, and the leafing phenology of the warm-season species common to the three grasslands. Apparently the general soil differences, though substantial, have not been sufficient to provide a stimulus for ecotypic differentiation *in the presence of the grazing animal* over the past 100 years.

References

BIDDISCOMBE, E. F., 1953.—A survey of the natural pastures of the Trangie District, New South Wales, with particular reference to the grazing factor. *Aust. J. agric. Res.*, 4 : 1–28.

BIDDISCOMBE, E. F., CUTHBERTSON, E. G., and HUTCHINGS, R. J., 1954.—Autecology of some natural pasture species at Trangie, N.S.W. *Aust. J. Bot.*, 2 : 69–98.

BURBIDGE, NANCY T., 1960.—The phytogeography of the Australian region. *Aust. J. Bot.*, 8 : 75–212.

BUTLER, B. E., and JOHNSTON, E. J., 1946.—A report on a detailed soil survey of Falkiner Memorial Field Station. *Coun. Sci. Industr. Res. Aust. Div. Soils Rep.* (Mimeo.)

CHURCHWARD, H. M., 1958.—The soils and land use of the Denimein Irrigation District, New South Wales. *C.S.I.R.O. Aust. Soils and Land Use Ser.*, No. 27.

CLARKE, C. M. H., 1968.—Flowering periods of alpine plants at Cupola Basin, Nelson, New Zealand. *N.Z. J. Bot.*, 6 : 205–220.

DERRICK, EDITH A., 1962.—Relative importance of various plants in causation of hayfever and asthma in Australia. *Med. J. Aust.*, 1 : 972–977.

GROVES, R. H., 1965a.—Growth of heath vegetation. II. The seasonal growth of a heath on a ground-water podzol at Wilson's Promontory, Victoria. *Aust. J. Bot.*, 13 : 281–289.

———, 1965b.—Growth of *Themeda australis* tussock grassland at St. Albans, Victoria. *Aust. J. Bot.*, 13 : 291–302.

GROVES, R. H., and SPECHT, R. L., 1965.—Growth of heath vegetation. I. Annual growth curves of two heath ecosystems in Australia. *Aust. J. Bot.*, 13 : 261–280.

HAVILAND, E., 1886.—Flowering seasons of Australian plants. *Proc. Linn. Soc. N.S.W.*, 11 : 1049–1051.

HEYWARD, JEAN, 1931.—Flowering periods of Victorian plants. *Proc. roy. Soc. Vic.*, 43 (n.s.) : 154–165.

HOLLAND, P. G., 1968.—Seasonal growth of field layer plants in two stands of mallee vegetation. *Aust. J. Bot.*, 16 : 615–622.

JOHNSTON, E. J., 1953.—Pedology of the Deniboota Irrigation District, New South Wales. *C.S.I.R.O. Aust. Soils Publ.*, No. 1.

JOHNSON, L. A. S., and BRIGGS, BARBARA G., 1963.—Evolution in the Proteaceae. *Aust. J Bot.*, 11 : 21–61.

MAIDEN, J. H., 1909.—A plea for the study of phenological phenomena in Australia. *J. Proc. roy. Soc. N.S.W.*, 43 : 157–170.

MOORE, C., 1880.—Anniversary address. *J. Proc. roy. Soc. N.S.W.*, 14 : 1–18.

MOORE, C. W. E., 1953a.—The vegetation of the south-eastern Riverina, New South Wales. I. The climax communities. *Aust. J. Bot.*, 1 : 485–547.

———, 1953b.—The vegetation of the south-eastern Riverina, New South Wales. II. The disclimax communities. *Aust. J. Bot.*, 1 : 548–567.

PATTON, R. T., 1933.—Ecological studies in Victoria—The Cheltenham flora. *Proc. roy. Soc. Vic.*, 45 (n.s.) : 205–218.

———, 1936.—Ecological studies in Victoria. IV. Basalt plains association. *Proc. roy. Soc. Vic.*, 48 (n.s.) : 172–191.

SCOTT, D., 1960.—Seasonal behaviour of some montane species. *N.Z. J. Sci.*, 3 : 694–699.

SMITH, R., 1945.—Soils of the Berriquin Irrigation District, N.S.W. *Coun. Sci. Industr. Res. Aust. Bull.*, No. 189.

SPECHT, R. L., 1957.—Dark Island Heath (Ninety-Mile Plain, South Australia). V. The water relationships in heath vegetation and pastures on the Makin sand. *Aust. J. Bot.*, 5 : 151–172.

———, 1958. The geographical relationships of the flora of Arnhem Land. *Amer.-Aust. Sci. Expedit. to Arnhem Land*, 3 : 415–442.

SPECHT, R. L., and RAYSON, PATRICIA, 1957.—Dark Island Heath (Ninety-Mile Plain, South Australia). I. Definition of the ecosystem. *Aust. J. Bot.*, 5 : 52–85.

STACE, H. C. T., HUBBLE, G. D., BREWER, R., et al., 1968.—*A Handbook of Australian Soils*. Rellim. Tech. Publ., Glenside, South Australia.

TWENTYMAN, R. L., 1938.—Pasture improvement. *J. Dept. Agric. Vic.*, 36 : 155–170, 197–204.

WILLIAMS, O. B., 1955.—Studies in the ecology of the Riverine Plain. I. The gilgai microrelief and associated flora. *Aust. J. Bot.*, 3 : 99–112.

———, 1956.—Studies in the ecology of the Riverine Plain. II. Plant-soil relationships in three semi-arid grasslands. *Aust. J. agric. Res.*, 7 : 127–139.

———, 1961.—Studies in the ecology of the Riverine Plain. III. Phenology of a *Danthonia caespitosa* Gaudich. grassland. *Aust. J. agric. Res.*, 12 : 247–259.

———, 1968.—Studies in the ecology of the Riverine Plain. IV. Basal area and density changes of *Danthonia caespitosa* Gaudich. in a natural pasture grazed by sheep. *Aust. J. Bot.*, 16 : 565–578.

———, 1969.—Studies in the ecology of the Riverine Plain. V. Plant density response of species in a *Danthonia caespitosa* grassland to 16 years of grazing by Merino sheep. *Aust. J. Bot.*, 17 : 255–268.